

ENVIRONMENTAL RESPONSES OF ACTIVE LIZARDS AT SARATOGA SPRINGS, DEATH VALLEY, CALIFORNIA

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Abstract.—Four species of lizards (*Uta stansburiana*, *Callisaurus draconoides*, *Cnemidophorus tigris*, and *Dipsosaurus dorsalis*) were studied at Saratoga Springs, Death Valley National Monument, California, during their seasons of activity. Effects of the environment on activity, and on seasonal and diel changes in body temperature were observed. The lizards were found to respond differently to the environmental factors of air temperature, substrate temperature, black-bulb temperature, wind, rain, and cloud cover. Temperature is the factor primarily affecting activity in all species. Seasonal acclimatization of T_b is suggested in *Uta* and *Dipsosaurus*. Diel thermal lability is shown in *Uta*, *Callisaurus*, and *Cnemidophorus*. The species appear to be effectively partitioned within the thermal environmental factors studied.

INTRODUCTION

In recent years there have been a number of studies treating the responses of lizards to the environment. Most of these studies have dealt largely or entirely with thermal relations. Among early studies are those of Conant (1938), Sergeev (1939), Cowles (1941), Cowles and Bogert (1944), and Fitch (1956). More recently, students of reptilian ecology have examined various interrelationships between environmental temperatures, taxonomic groups, and body temperatures of lizards. Among these are the studies of Milstead (1957a), Ruibal (1961), and Soulé (1963). Heath (1962, 1964, 1965) has examined thermoregulation of *Phrynosoma* in some detail, and Bustard (1967) has done similar work on *Gehyra variegata*. Milstead (1957b) and Laughlin (1965) included thermal relations in their studies of competitive interactions of lizards. Miller and Stebbins (1964) presented data on environmental responses of vertebrates in Joshua Tree National Monument, California, and Brattstrom (1965) and Cunningham (1966) have presented summaries of body temperatures of various reptiles.

This study was undertaken to determine the relationship of certain components of the environment to the body temperature and activity of *Uta stansburiana*, *Callisaurus draconoides*, *Cnemidophorus tigris*, and *Dipsosaurus dorsalis* at Saratoga Springs, Death Valley National Monument, California. The environmental components chosen were air temperature, substrate temperature, black-bulb temperature, wind, rain, and cloud cover. Wherever possible, reactions to these components have been correlated with time of day and season. It has been made apparent, from the studies cited above, that these factors are all of major importance in the ecology of lizards, especially desert forms. I have examined the reactions of the in-

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dividual species to these components and compared reactions between species to determine whether ecological segregation has occurred.

STUDY AREA

Location:

Saratoga Springs lies in the extreme southern portion of Death Valley National Monument, San Bernardino Co., California, at an elevation of 59.1 m. The springs are ca. 60.0 km NNW of Baker, San Bernardino Co., California; ca. 29.6 km SW of Shoshone, Inyo Co., California; and ca. 80.0 km ssw of Furnace Creek, D.V.N.M., Inyo Co., California. The study area is bounded on the west by the Amargosa River and attendant alkali flats, and on the north, south, and east by rocky ridges of the Ibex Mountains. A narrow strand of creosote desert at the northwest end of the study area connects with an extensive alluvial fan-creosote desert area to the north.

Description:

The study area consists of a spring pond fed by two constant temperature spring heads; three smaller non-impounded, constant temperature springs that drain into a three-acre, seasonally fluctuating marsh; a rim of dunes; a small alluvial fan; and the rocky ridges (Deacon, et al, mimeographed report). The dunes, alluvial fan, and to a lesser extent the ridges and dry portions of the marsh are considered in this study. The plant communities of Saratoga Springs are discussed in some detail by Bradley (1970).

Climate:

Freezing temperatures are limited to December and January, and summer temperatures regularly exceed 43.0 C. Table 1 is a summary of temperature data for the period of the study. U. S. Weather Bureau records from the station 14.4 km NNW of Baker, San Bernardino Co., Calif., the nearest weather station, recorded 1.06 cm of rain in 1967, more than half of which fell in winter and spring.

Table 1. Summary of ambient temperature at Saratoga Springs, D.V.N.M., San Bernardino Co., California, for February 1967-June 1968. Sample intervals represent first and last week in each month and the range is in parenthesis.

Sample Interval	X Max. °C	X Min. °C	X °C
1-7 February	28.4	7.0	17.8
1967	(26.7-30.0)	(4.4-8.9)	(4.4-30.0)
22-28 February	21.6	4.2	13.0
1967*	(20.0-24.0)	(1.7-7.2)	(1.7-24.0)
1-7 March	24.3	5.8	14.8
1967*	(16.6-28.9)	(2.2-9.4)	(2.2-28.9)
25-31 March	23.4	8.9	16.3
1967*	(17.8-28.4)	(2.6-12.8)	(2.6-28.4)
1-7 April	21.8	7.5	14.7
1967*	(16.2-26.1)	(4.0-10.6)	(2.0-26.1)
21-27 April	34.1	11.5	24.4
1967	(28.3-41.7)	(8.3-15.5)	(8.3-41.7)
28 April-4 May	34.3	14.1	25.2
1967	(30.0-39.3)	(11.2-20.0)	(11.1-39.3)

Table 1. (Continued)

Sample Interval	X Max. °C	X Min. °C	X °C
25-31 May	32.7	17.6	25.1
1967*	(27.3-37.3)	(11.1-20.0)	(11.1-37.3)
1-7 June	31.8	15.7	23.9
1967*	(26.0-35.0)	(11.7-17.8)	(11.7-35.0)
24-30 June	42.4	24.0	33.0
1967*	(40.5-46.2)	21.1-28.3)	(21.1-46.5)
1-7 July	45.1	27.9	36.6
1967*	(41.1-48.4)	(23.3-31.6)	(23.3-48.4)
25-31 July	43.0	28.6	35.2
1967*	(39.3-45.5)	(26.7-30.6)	(26.7-45.5)
1-7 August	43.0	27.5	35.3
1967*	(40.6-45.0)	(24.4-30.6)	(24.4-45.0)
25-31 August	41.8	25.5	32.8
1967	(37.8-45.0)	(23.3-27.8)	(23.3-45.0)
2-6 September	44.8	28.3	37.5
1967‡	(41.1-48.8)	(24.5-32.2)	(24.5-48.8)
24-30 September	30.3	26.2	30.1
1967	(16.0-37.3)	(23.8-28.8)	(16.0-37.3)
1-7 October	32.8	24.3	28.6
1967	(30.4-34.4)	(21.1-26.7)	(21.1-34.4)
25-31 October	34.1	17.5	25.6
1967	(27.8-37.3)	(12.8-18.3)	(12.8-37.3)
1-7 November	32.9	17.2	24.8
1967	(29.4-35.0)	(14.3-20.0)	(14.3-35.0)
24-30 November	18.3	7.3	12.9
1967	(12.7-21.1)	(4.4-10.0)	(4.4-21.1)
1-7 December	17.0	5.6	11.9
1967	(14.4-21.1)	(3.3-17.7)	(3.3-21.1)
25-31 December	18.3	1.3	9.7
1967*	(15.0-21.1)	(-2.2-15.6)	(-2.2-21.2)
1-7 January	14.0	-2.4	5.8
1968*	(13.2-15.0)	(-5.6-2.8)	(-5.6-15.0)
25-31 January	22.1	7.3	14.6
1968	(18.9-24.5)	(3.4-12.8)	(3.4-24.5)
1-7 February	24.8	5.8	15.2
1968	(21.6-27.6)	(4.0-8.3)	(4.0-27.6)
24-29 February	34.3	15.0	25.3
1968‡	(32.2-36.2)	(10.6-16.6)	(10.6-36.2)
1-7 March	31.6	12.7	21.4
1968	(24.4-35.5)	(9.6-15.5)	(9.6-35.5)
25-31 March	29.4	10.8	20.3
1968*	(27.8-32.1)	(7.2-14.4)	(7.2-32.1)
1-7 April	37.0	15.2	26.2
1968	(35.0-39.4)	(13.7-21.1)	(13.7-39.4)
24-30 April	45.5	17.6	31.6
1968	(43.2-49.4)	(15.5-20.4)	(15.5-49.4)
1-7 May	46.2	22.0	34.4
1968	(41.6-50.4)	(18.3-25.0)	(18.3-50.4)
25-31 May	39.4	19.5	29.3
1968*	(34.0-41.8)	(16.7-23.3)	(16.7-41.8)
1-7 June	35.9	20.6	28.0
1968*	(27.2-42.7)	(15.0-26.7)	(15.0-42.7)
24-30 June	42.3	24.3	33.4
1968*	(38.3-45.6)	(21.7-27.2)	(21.7-45.6)

*Records from U.S. Weather Bureau Station, 14.4KM NNW, Baker, San Bernardino Co., California.

‡One day's minimum temperature missing.

MATERIAL AND METHODS

Most lizards were collected by shooting with .22 caliber "dust shot." Noosing or hand capture was used to a lesser extent. Collections were made during at least one day per month from February 1967 to June 1968, except May, June, November, and December 1967.

Data recorded included the following: 1) species, 2) sex, 3) body temperature (T_b), 4) substrate temperature (T_s), 5) air temperature (T_a), 6) wind speed taken within 5 cm of the substrate, 7) time of day in PST, 8) habitat, and 9) black-bulb temperature (T_{BBT}). Black-bulb temperatures were not taken during the second half of the study. All other temperatures were taken as outlined by Brattstrom (1965), except in June 1968 when a standard mercury thermometer was used to measure T_s because of the 50 C limit imposed by the Schultheis thermometer. Wind speed was measured with a hand-held Dwyer wind meter calibrated in mph. Measurements were made as close as possible to the site of capture and in the order 1) T_b , 2) T_a , 3) T_s and T_{BBT} , and 4) wind speed.

Records of general ambient temperature were obtained from recording thermographs maintained in the field. The records obtained were not complete, however, due to occasional machine failure. Missing data have been supplemented by use of U.S. Weather Bureau records from the station 14.4 km NNW Baker, Calif.

All quantitative data for each lizard were analyzed statistically on an IBM 1130 computer. Statistical values used in this study represent the 5% level of confidence and means are presented \pm one standard error of the mean unless stated otherwise.

RESULTS

Uta stansburiana:

The side-blotched lizard is active within a wide range of environmental conditions at Saratoga Springs. Temperature exerts a primary control over activity of *Uta*, and other factors seem of importance only so far as they affect temperature.

Uta stansburiana at Saratoga Springs have been collected over a wide range T_a and T_s (Table 2). Low temperature values recorded here are somewhat lower than those listed by Brattstrom (1965). T_b of *Uta* correlates more closely to T_a than T_s (T_a , $r = .598$, $df = 90$, $P < .01$; T_s , $r = .396$, $df = 90$, $P < .01$). Table 2 indicates \bar{X} that mean body temperature (MBT) is closer to $\bar{X} T_s$ than $\bar{X} T_a$. The range of T_s is greater than that of T_b , especially at higher temperatures, and is probably the reason for the higher T_b : T_a correlation. My observations differ from those of Soulé (1963) who found no correlation between T_b and T_a for *Uta* from Baja California, Mexico.

T_{BBT} associated with active *Uta* ranged from 25.1 C to 47.6 C ($\bar{X} = 35.85 \pm .76$ C).

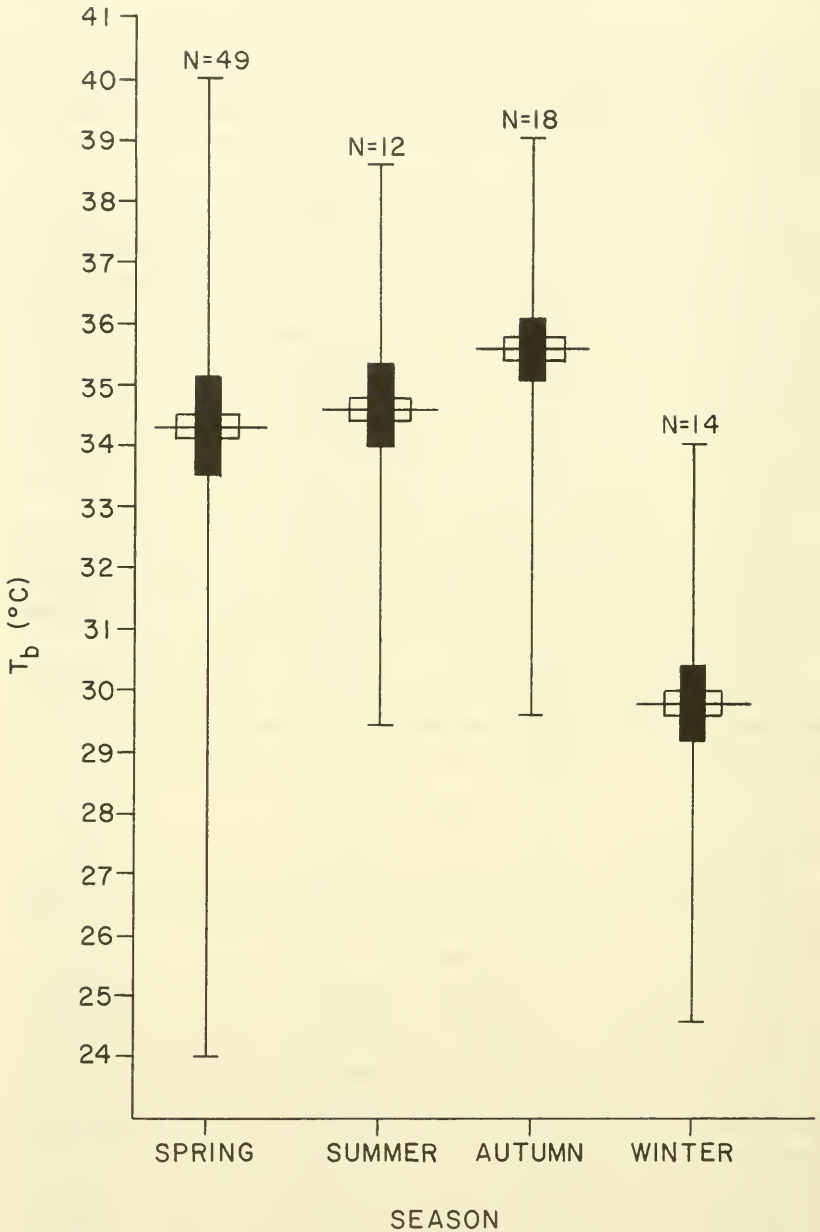


Fig. 1. A comparison, by season, of the range and mean of T_b for *Uta stansburiana* at Saratoga Springs, D.V.N.M., California. Vertical line is range; Horizontal line is \bar{X} ; Vertical bar is 2S; Horizontal bar is 2S_x.

Table 2. Summary of temperature data obtained from four lizard species at Saratoga Springs, D.V.N.M., California. Mean $\pm 1 S_x$, range in parenthesis, and sample size.

	°C	All Parameters		♂	♀	Spring	Summer	Autumn	Winter
		N = 92	N = 55						
Uta	T _b	33.84 \pm .40 (24.6-40.0)	34.31 \pm .49 (24.6-40.0)	N = 37	33.15 \pm .67 (24.0-39.8)	N = 49	N = 12	N = 18	N = 14
	T _s	32.84 \pm .59 (21.0-47.4)	32.13 \pm .83 (21.6-44.6)		33.84 \pm .87 (23.0-47.4)	34.32 \pm .57 (24.0-40.0)	34.55 \pm .87 (29.4-38.6)	35.61 \pm .60 (29.6-39.0)	29.82 \pm .77 (24.6-34.2)
	T _a	30.72 \pm .45 (18.0-39.6)	30.54 \pm .65 (18.0-38.6)		31.00 \pm .69 (21.6-39.6)	34.37 \pm .93 (23.0-47.4)	33.78 \pm .92 (29.1-40.0)	32.68 \pm 1.27 (24.4-43.1)	27.95 \pm 1.33 (21.0-39.8)
Callisaurus	T _b	N = 80	N = 40	N = 40		31.75 \pm .56 (22.6-39.6)	32.88 \pm .77 (28.8-38.6)	31.55 \pm .88 (25.6-36.4)	24.42 \pm .92 (18.0-28.8)
	T _s	39.00 \pm .40 (26.2-43.8)	38.70 \pm .56 (26.2-43.2)		39.31 \pm .57 (31.5-43.8)	N = 44	N = 21	N = 14	
	T _a	42.23 \pm .70 (21.8-51.0)	40.67 \pm .90 (26.1-49.8)		41.78 \pm 1.08 (21.8-51.0)	39.49 \pm .46 (32.0-43.8)	38.37 \pm .96 (26.2-43.2)	38.26 \pm 1.00 (30.0-42.0)	
Draconoides	T _b	36.51 \pm .49 (22.4-45.4)	36.04 \pm .60 (26.8-42.8)		36.97 \pm .77 (22.2-46.4)	42.30 \pm .94 (21.8-51.0)	40.43 \pm 1.44 (26.1-50.8)	38.41 \pm 1.26 (31.4-46.2)	
	T _s	N = 47	N = 29	N = 18		36.52 \pm .66 (22.2-42.8)	37.89 \pm 1.05 (26.8-45.4)	34.61 \pm .81 (29.2-40.0)	
	T _a	39.72 \pm .30 (34.4-42.4)	39.76 \pm .38 (34.4-42.4)		39.66 \pm .49 (36.0-42.4)	N = 30	N = 16		
Cnemidophorus	T _b	39.34 \pm .82 (25.0-50.0)	38.88 \pm .84 (30.8-49.8)		40.08 \pm 1.68 (25.0-50.0)	40.11 \pm 1.12 (25.0-50.0)	37.65 \pm 1.06 (32.3-47.8)		
	T _s	34.99 \pm .60 (25.4-44.8)	35.24 \pm .69 (27.8-44.8)		34.60 \pm 1.13 (25.4-43.6)	34.68 \pm .79 (25.4-44.8)	35.89 \pm .95 (29.8-43.6)		
	T _a	N = 44	N = 16	N = 28		N = 33	N = 11		
Dipsosaurus	T _b	40.20 \pm .31 (35.2-43.2)	40.00 \pm .39 (37.0-42.2)		40.31 \pm .44 (35.2-43.2)	39.73 \pm .36 (35.2-43.0)	41.58 \pm .42 (39.0-43.2)		
	T _s	42.14 \pm .78 (27.8-50.2)	40.94 \pm 1.46 (27.8-50.2)		42.83 \pm .89 (32.4-50.1)	42.27 \pm .53 (27.8-50.2)	41.76 \pm 1.48 (36.2-50.1)		
	T _a	37.69 \pm .55 (28.2-46.8)	36.69 \pm .88 (28.2-42.0)		38.26 \pm .70 (28.8-46.8)	37.21 \pm .68 (28.2-46.8)	39.16 \pm .71 (36.4-42.6)		

No *Uta* was found active during this study at a T_s higher than 47.4 C or a T_a higher than 39.6 C, although temperatures in excess of T_s 50.0 C and T_a 45.0 C are commonly available. On 30 July 1967 the low T_a measured at ca. 0500 hrs. PST was in excess of 30.0 C and the high, measured at 1740 hrs., was 44.1 C. Only one *Uta* was seen that day (0625 hrs.; T_a , 35.9 C; T_s , 36.0 C).

During the hotter months of the year, the rocky hillsides are almost devoid of *Uta*, even in the early morning. It is possible that in the summer the rocks constantly maintain surface temperatures in excess of 35.0 C. Because of difficulties of obtaining accurate measurements of rock surface temperatures, this possibility was not tested. The sudden reappearance of numerous adult *Uta* in the rocky area with the advent of cooler autumn temperatures seems to suggest that a portion of the population at Saratoga Springs may estivate.

Wind speed has a negative effect on T_b ($r = -.268$, $df = 90$, $P = .01$). Gusts up to 16.0 kph do not seem to affect activity appreciably, but constant wind over 8.0-16.0 kph apparently stops or reduces activity. The species has been collected within a range of wind speeds from 0.0-12.0 kph ($X = 2.67 \pm .30$ kph).

Rain negatively affects the activity of *U. stansburiana*. Light, intermittent rain will briefly curtail activity, but as soon as the sun reappears, activity resumes. Constant light, heavy, or cold rain will stop all activity. Cloud cover can also reduce or stop activity, especially if a distinct lowering of temperature ensues.

Seasonal thermal responses, especially during winter, differ sufficiently to warrant discussion. During spring and autumn, unless it rains, *Uta* are probably active every day. During summer they are active at least part of every day, unless habitat temperatures exceed 30.0-40.0 C for the entire day. In winter *Uta* appear to be active on any day that has an ambient temperature greater than 20.0 C, and is sufficiently clear to allow them to bask. Pearson (1954) has demonstrated that a lizard, *Liolaemus multiformis*, living at high elevations in Peru can achieve a T_b high enough for activity even when ambient temperature is near freezing, if sufficient insolation is available. Cunningham (1966) reported finding *Uta* basking at T_b 14.5 C and T_s 15.0 C. Cowles (1941) reported finding *Uta* active during February 1937, "... an exceptionally cold winter." Tinkle (1967) reported *Uta* active on any warm day throughout the year. Brattstrom (1965) reported T_b 's of *Uta* collected from February to September, and found no significant differences between them.

In January 1968 a field experiment was performed to determine the minimum temperature at which *Uta* could survive and show coordinated locomotor activity. Six animals were placed in a one gallon glass jar and left overnight. The lizards were examined early the following morning and T_a inside the bottle measured. All of the lizards were alive and T_b was measured for three of them. T_a in the bottle was 4.2 C and the T_b 's were 8.2, 4.2, and 4.2 C. The lizard with the high T_b was handled slightly longer than the others. The

lizards were returned to the bottle, left for 0.5 hrs., and measured again. The bottle was then placed in the sunlight and left for an additional 20 min. T_a inside the bottle, T_b of three lizards, and observations on locomotor activity were recorded at each interval.

At T_b 4.2 C the lizards were able to move stiffly when prodded and tended to arch their tails when handled. The tails remained rigidly arched over the lizards' backs when they were put down. At T_b 7.0-8.4 C (T_a = 6.4 C) slow, coordinated movements occurred and the lizards attempted to escape when handled. When the bottle was placed in the sun, temperatures rose rapidly and most of the lizards attempted to bask by orienting maximum surface area toward the sun. At the last measurement the T_a was 10.6 C and three T_b 's were 20.6, 18.6, and 16.6 C. The lizards at T_b 20.6 and 18.6 C were very active and apparently capable of normal locomotor activity. The lizard at 16.6 C was slightly more sluggish. These temperatures agree with the voluntary minimum T_b 's listed by Cunningham (1966), who found *Uta* basking at T_b 9.5-19.2 C. Tinkle (1967) recorded seeing *Uta* active in winter at T_a 4.0 C, but more often at T_a greater than 10.0 C. It appears that emergence temperature of *Uta* may be as low as T_b 7.0 C and T_a ca. 7.0 C since lizards are capable of coordinated movement at those temperatures, and have been observed basking at T_b 9.5 C (Cunningham, 1966).

MBT's of *U. stansburiana* collected in spring (Feb.-April), summer (May-July), and autumn (Aug.-Oct.) do not differ significantly (Table 3), but there appears to be a tendency toward an increase from spring to autumn (Fig. 1). T_b , T_s , and T_a for winter (January) animals are significantly lower than for any other season (Table 3), a situation also observed by Roberts (1968). The difference in environmental temperatures is to be expected, with low temperatures generally being the only ones available in the environment in winter. The reduction in T_b would not necessarily be expected (Dawson and Bartholomew, 1956).

Diel thermal lability varies seasonally in *Uta* at Saratoga Springs. The correlation of T_b with time of day is very weak in spring, approaches significance in summer (r = .501, df = 10, P > .05), and is strong in autumn (r = .589, df = 16, P < .05) with T_b tending to be higher in the afternoon than in the morning (Fig. 3). T_b does not correlate with time of day in winter-collected lizards.

Callisaurus draconoides:

Callisaurus draconoides also respond primarily to temperature and have been collected over a wide range of temperatures (Table 2). T_b of *Callisaurus* correlates slightly higher with T_s than T_a (T_a , r = .716, df = 78, P < .01; T_s , r = .794, df = 78, P < .01). Soulé (1963) found a lower, but significant correlation between T_b and T_a in *Callisaurus* studied by him. *Callisaurus* are found active at Saratoga Springs when every other species studied has sought shelter from the heat. Norris (1967) discusses the mechanisms enabling *Callisaurus* to maintain activity at high temperatures. Apparently 20.0 C is the lowest T_a or T_s that will be voluntarily tolerated by

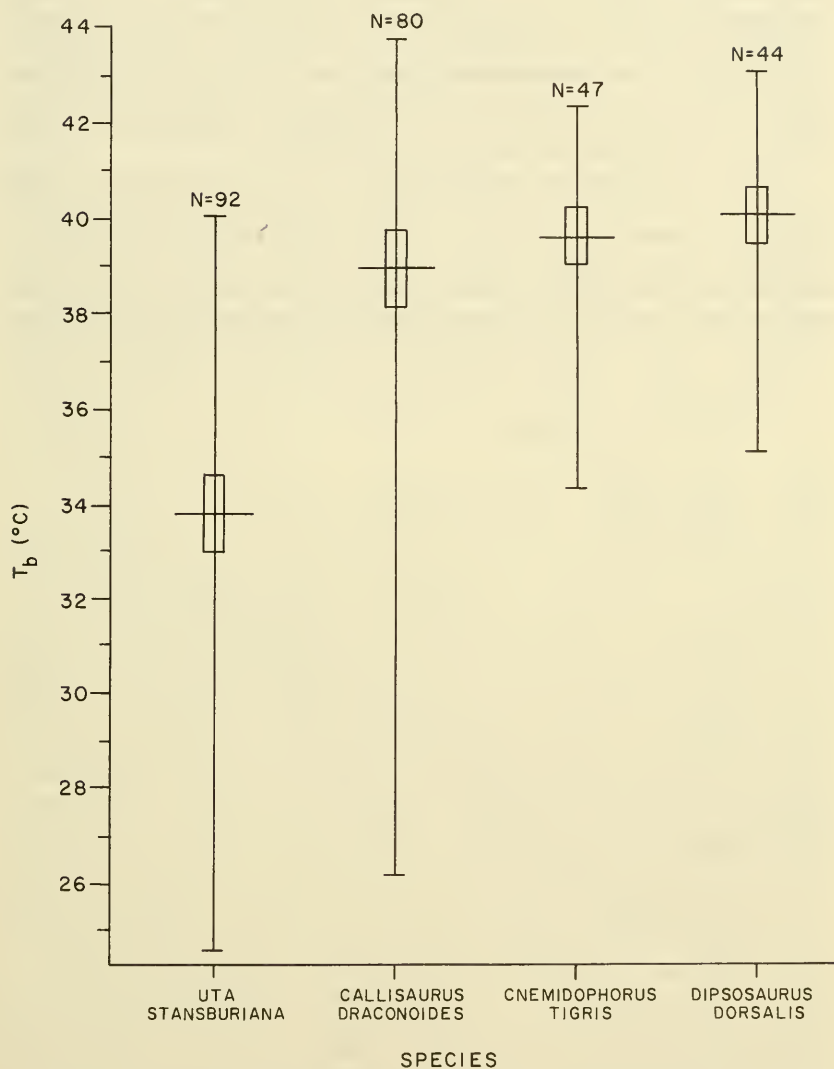


Fig. 2. A comparison of MBT of four species of active lizards from Saratoga Springs, D.V.N.M., California. Vertical line is range; Vertical bar is $2S_X$.

Callisaurus. I have only three records of *C. draconoides* active at T_a less than 30.0 C and two records of T_s less than 30.0 C. These records probably represent lizards that had just emerged since they are generally from early in the day and are scattered throughout the activity season (Table 2). Brattstrom (1965) lists 26.4-31.5 C as the T_b of emerging *Callisaurus* and Soulé (1963) lists 22.0 C as the

minimum T_a . The voluntary minimum T_b determined in a laboratory gradient is 29.8 C (R. Clark and W. G. Bradley, unpubl. data). The MBT of *Callisaurus* (Table 2) from this study does not appear to differ from that reported by Brattstrom (1965) or Cunningham (1966). The ranges of T_b observed are similar to those author's, except that my maxima are 3.6 C higher than Brattstrom's (1965) and 1.4 C higher than Cunningham's (1966).

I found no significant difference in T_b between the sexes (Table 3). T_{BBT} associated with active *Callisaurus* does not appear to differ significantly from T_s (T_{BBT} , $\bar{X} = 42.15 \pm .93$ C; range, 34.0-50.8 C).

Other environmental factors that influence the activity of *C. draconoides* (wind, rain, cloud cover) are similar to those for *Uta stansburiana*. Smith (1946) noted that *Callisaurus* bury themselves just under the surface of the sand during light rains. My observa-

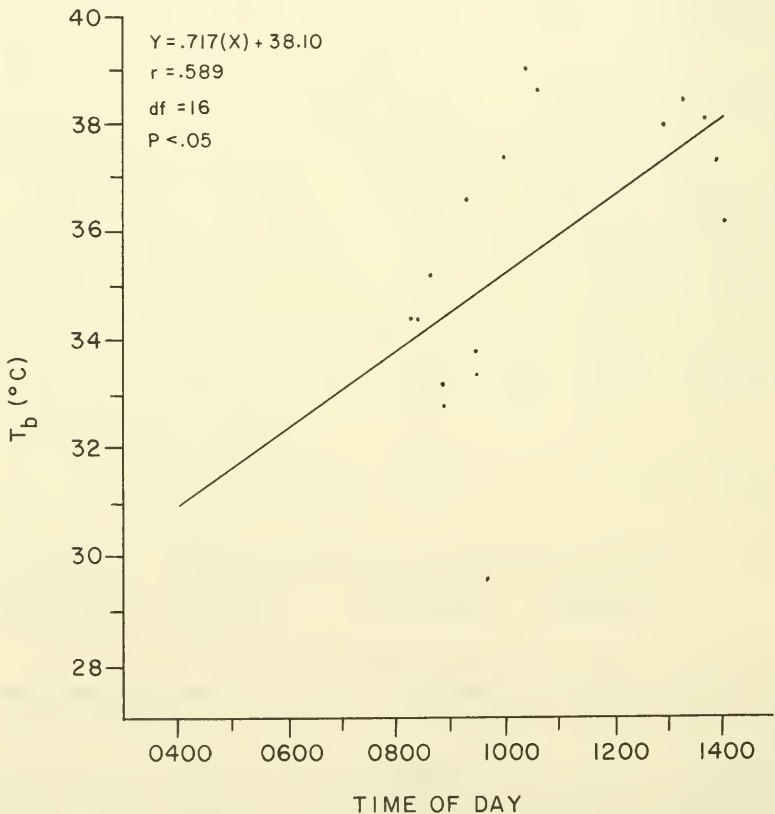


Fig. 3. Scatter diagram of T_b on time of day for *Uta stansburiana* in autumn at Saratoga Springs, D.V.N.M., California. Line fit by method of least squares. Regression equation, correlation coefficient (r), degrees of freedom (df), and significance level (P) are indicated.

tions tend to support this inasmuch as *Callisaurus* reappear very shortly after rain ceases. Moderate to heavy cloud cover can reduce activity and, if associated with a large temperature drop, stop it altogether. Zebra-tailed lizards have been collected at wind speeds up to 11.2 kph, and gusts up to 19.2 kph seem to have little effect on activity. Steady wind in excess of 8.0 kph, however, reduces or stops activity. Wind seems to have a negative effect on T_b ($r = -.117$). The mean wind speed at which *Callisaurus* has been collected is $3.09 \pm .35$ kph (range, 0.0-11.2 kph).

The MBT of *Callisaurus* does not differ significantly between the seasons (Table 3). T_b 's of autumn *Callisaurus* are only slightly lower than those of spring and summer (Table 2). Diel thermal lability has been observed only in summer-collected lizards. The correlation between T_b and time of day for summer-collected animals is highly significant ($r = .660$, $df = 19$, $P < .01$). There is a strong trend toward an increase in T_b in the afternoon (Fig. 4). *Callisaurus* has not been observed during winter at Saratoga Springs. *Cnemidophorus tigris*:

Several previous authors including Cowles (1940, 1941), Milstead (1957a, b), Miller and Stebbins (1964), Bostic (1966, 1968), Medica (1967), and Echternacht (1967) have studied the environmental responses and thermal relations of *C. tigris* and other species of the genus. *Cnemidophorus tigris* are most active at moderate temperatures. Table 2 shows the range and MBT for the *Cnemidophorus* collected during this study. The MBT is lower than that listed by Brattstrom (1965). There is no significant difference in MBT of male and female whiptails (Table 3). The lowest T_s at which *C. tigris* was collected in this study (25.0 C) is 3.0 C and 5.0 C lower than those reported by Milstead (1957a) and Echternacht (1967) respectively. The highest T_s recorded in this study (50.0 C) corresponds to the data of Milstead (1957a), but is higher than that reported by Echternacht (1967). Milstead (1957a) and Medica (1967) indicate that *Cnemidophorus* activity ceases when T_s reaches 50.0 C in the areas studied by them and that activity can be modified by changes in daily weather that modify temperature. My observations indicate that the same is true at Saratoga Springs.

T_b correlates higher with T_s than T_a when my data are lumped, but both correlations are significant (T_s , $r = .506$, $df = 45$, $P < .01$; T_a , $r = .422$, $df = 45$, $P < .01$). These data agree with those of Milstead (1957a), Medica (1967), and Echternacht (1967). Milstead's (1957a) data apparently did not show such a high correlation between T_b and T_a however. The mean T_{BBT} at which *C. tigris* has been collected is 44.50 ± 2.74 C (range, 36.0-51.8 C). The mean is based on a small sample ($n = 6$), but seems to agree with the data of Milstead (1957a) and Degenhardt (1966).

There is no indication of a negative relation between wind speed and T_b for *C. tigris* collected at Saratoga Springs ($r = .027$). This may be a reflection of the species' propensity for rather dense vegetative cover. *Cnemidophorus* have been collected over a range of

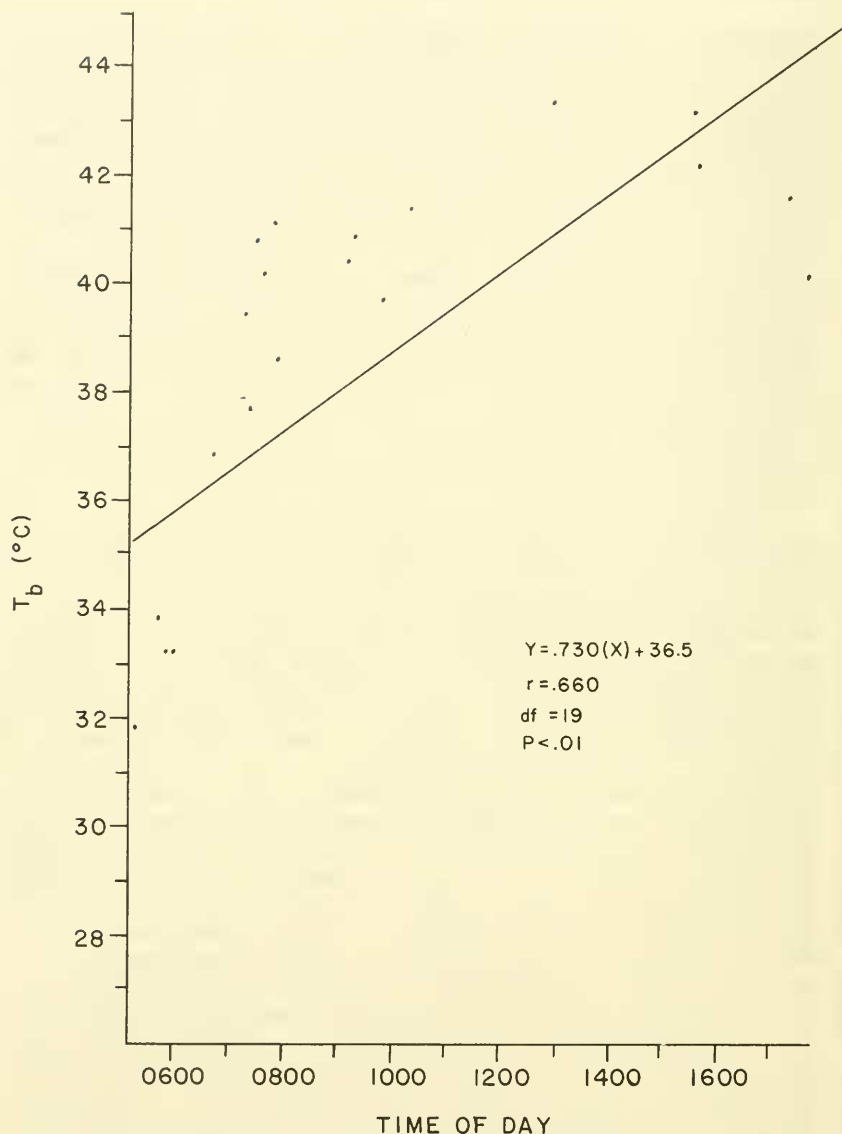


Fig. 4. Scatter diagram of T_b on time of day for *Callisaurus draconoides* in summer at Saratoga Springs, D.V.N.M., California. Line fit by method of least squares. Regression equation, correlation coefficient (r), degrees of freedom (df), and significance level (P) are indicated.

wind speed of 0.0-12.8 kph ($X = 2.90 \pm .51$ kph). Apparently wind speeds in excess of 12.8 kph cause *C. tigris* at Saratoga Springs to retreat underground or to dense cover. Echternacht (1967) reported that wind had no effect on *C. tigris* studied by him.

I have no data on the effect of cloud cover or rain on *Cnemidophorus* activity. Bostic (1966, 1968) and Echternacht (1967) report that heavy cloud cover or rain has a direct and deleterious effect on activity of *Cnemidophorus* studied by them.

There is a seasonal difference in MBT of active whiptails. MBT in spring is significantly higher than in summer (Table 3). Since autumn data are available for only one lizard, no comparison can be made with that season. No previous author has reported seasonal differences in MBT of active *Cnemidophorus*.

The correlation of T_b to environmental temperatures differs between spring and summer-collected *C. tigris* at Saratoga Springs. T_b of summer-collected whiptails correlates higher with T_a than T_s , though both are significant (T_a , $r = .734$, $df = 14$, $P < .01$; T_s , $r = .499$, $df = 14$, $P = .05$). Spring-collected lizards have a higher $T_b:T_s$ correlation (T_s , $r = .485$, $df = 28$, $P < .01$; T_a , $r = .386$, $df = 28$, $P < .05$). I believe these correlations reflect the observation that whiptails are seen in open habitat more frequently during spring than during summer. No previous author seems to have observed a similar seasonal shift in correlation of T_b with environmental temperatures.

Diel thermal lability is found in *C. tigris* in spring and summer. T_b correlates significantly with time of day during both seasons (spring, $r = .369$, $df = 28$, $P < .05$; summer, $r = .534$, $df = 14$, $P < .05$). Although the trend toward an afternoon increase in T_b is evident, it is not as strongly marked as in *Callisaurus* or *Uta* (Fig. 5). *Dipsosaurus dorsalis*:

Dipsosaurus dorsalis, as noted by Norris (1953) and Brattstrom (1965), has the highest MBT of any North American lizard yet studied. The MBT and activity range of *Dipsosaurus* from Saratoga Springs are shown in Table 2. The activity range of T_b for *D. dorsalis* measured in this study is rather narrow and the values obtained for MBT and activity range agree with those of previous authors (Norris, 1953; Brattstrom, 1965; Cunningham, 1966). The MBT of *D. dorsalis* is significantly higher than *U. stansburiana* and *C. draconoides*, but not *C. tigris* (Table 3). The T_a and T_s at which *Dipsosaurus* are active is also high, due largely to time of activity. T_a and T_s are significantly higher than those associated with *Uta* and *Cnemidophorus*, but not *Callisaurus* (Table 3). T_b of *D. dorsalis* in this study correlates more highly with T_a than T_s (T_a , $r = .574$, $df = 42$, $P < .01$; T_s , $r = .305$, $df = 42$, $P = .05$).

Wind speed has a nonsignificant, but apparently negative effect on T_b ($r = -.272$). *Dipsosaurus dorsalis* seems to be more sensitive to wind than any other lizard studied at Saratoga Springs since it was never seen or collected at wind speeds in excess of 8.0 kph. The mean wind speed at which *D. dorsalis* has been collected is $2.61 \pm$

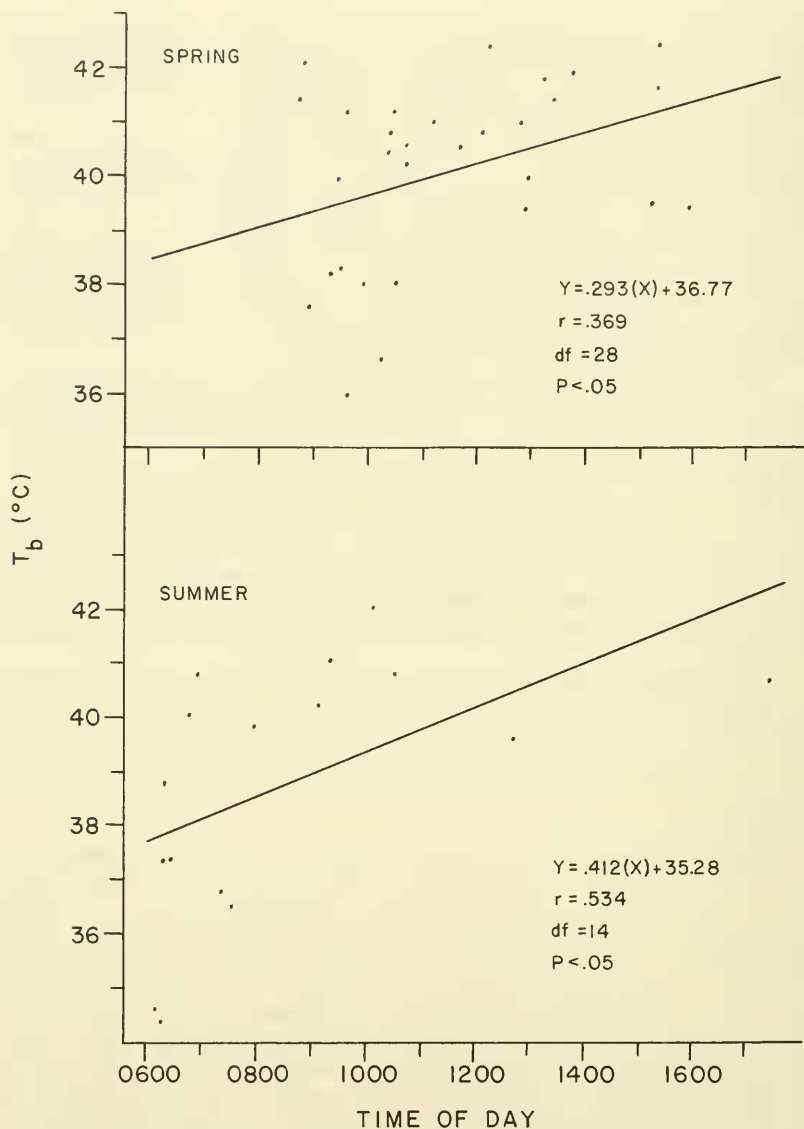


Fig. 5. Scatter diagrams of T_b on time of day for *Cnemidophorus tigris* in spring and summer at Saratoga Springs, D.V.N.M., California. Lines fit by method of least squares. Regression equation, correlation coefficient (r), degrees of freedom (df), and significance level (P) are indicated.

.66 kph (range, 0.0-8.0 kph). No data are available on the effect of rain or cloud cover on the activity of *D. dorsalis* at Saratoga Springs.

Examined seasonally, MBT of *Dipsosaurus* is significantly higher in summer than in spring (Table 3). I have no data on thermal responses of autumn lizards. There is no apparent diel thermal lability in *D. dorsalis* during any season.

DISCUSSION

Although my results, in many respects, resemble those of previous studies, several new relationships are reported. This study permits comparisons of the thermal niches of these four species in a situation in which each species has an equal opportunity to respond to the components examined. It seems, therefore, that any differences noted between the species should be a reflection of ecological separation within the components examined.

The lizards of Saratoga Springs all respond primarily to temperature. However, each species responds differently to the available thermal mosaic. Several measures of this differential response are available. Among them are comparison of MBT's of the species, relationships between activity and environmental temperatures, and diel or seasonal lability of T_b .

Examination of Figure 2 and column 1 of Table 2 reveals that the MBT differs between the species listed although some overlap of means occurs between three of the species. The MBT of *U. stansburiana* differs significantly from all of the other species. The low MBT of *Uta* reflects the species' utilization of the lower end of the thermal spectrum. The MBT of *Callisaurus* is significantly lower than that of *D. dorsalis*, but not of *C. tigris*. The MBT of *D. dorsalis* is significantly higher than any species except *C. tigris*. T_a and T_s associated with the species also differ (Table 3).

Cowles and Bogert (1944) and Degenhardt (1966) consider black-bulb temperature to describe the limits for lizard activity. T_{BBT} is measured in direct sunlight and represents the maximum temperature available at a particular time (Cowles and Bogert, 1944). It seems reasonable to conclude that a range of T_a of 18.0-40.0 C describes the thermal limits of activity for *Uta*. The corresponding range of T_{BBT} is 25.0-48.0 C. Since during the major part of the activity day T_a seems to be the temperature that has the greatest relationship to T_b of *Uta*, I feel that T_{BBT} is a measure of potential activity only during periods when the lizards are actively basking to raise T_b (early morning, late afternoon).

Degenhardt (1966) has shown that T_{BBT} is a very reliable indicator of activity in *Cnemidophorus* and *Holbrookia* studied by him. My values for *Cnemidophorus* correspond well with his. I feel that T_{BBT} is also a valid indicator of *Callisaurus* activity at Saratoga Springs. No data are available for *D. dorsalis*.

Ruibal (1961) and Licht (1968) have shown that several species

of *Anolis* have different thermal responses associated with daily photoperiod. These authors have shown changes in T_b , preferred T_b , and heat resistance correlated with photoperiod, both in the laboratory and in the field. Hutchison and Kosh (1965) and Kosh and Hutchison (1968) have demonstrated changes in resistance to high temperature in the turtle, *Chrysemys picta*, that are related to changes in photoperiod. Three species of lizards (*U. stansburiana*, *C. draconoides*, and *C. tigris*) studied at Saratoga Springs have diel shifts in T_b (Figs. 3, 4, 5).

In autumn, *U. stansburiana* has a marked increase in T_b in the afternoon (Fig. 3). This may reflect acclimatization to high daily temperatures in summer with residual effects being shown in autumn. Roberts (1968) found a slight elevation in MBT of summer-collected lizards, but found no change in O_2 consumption in lizards from spring through autumn, except in juvenals taken during June and July. *Callisaurus*, in summer, have an increased T_b in the afternoon (Fig. 4). This is probably a reflection of the propensity of the species for activity when ambient temperature and direct insolation are at their highest. Thermal lability in *C. draconoides* may be advantageous, as mentioned by Norris (1967), by allowing the species to be active when predators and competitors are in hiding. *Cnemidophorus* shows apparent diel thermal lability in spring and summer (Fig. 5). Apparently because summer temperatures are higher than those in spring, the elevation of T_b in summer is slightly greater than in the spring. Diel thermal lability in *C. tigris*, as in the other species discussed, seems to be an adaptation allowing slightly longer activity periods under sub-optimal conditions of temperature.

A number of authors, including Lowe and Vance (1955), Wilholt and Anderson (1960), Larson (1961), Mayhew (1963), and McGinnis (1960) have described seasonal changes in T_b of field-active lizards and changes in thermal tolerance after acclimation to both high and low temperatures in several species of lizards. Three species of lizards studied at Saratoga Springs (*U. stansburiana*, *C. tigris*, and *D. dorsalis*) have significant seasonal shifts in MBT (Tables 2 and 3).

Dipsosaurus dorsalis shows a shift which may represent acclimatization to increased temperature (Table 2, 3). *Cnemidophorus tigris* has a seasonal shift in MBT that is the reverse of that seen in *D. dorsalis* (Table 2). The increased MBT of spring-collected whiptails may reflect sampling error, or may be a reflection of higher thermal requirements or increased exposure during the reproductive season.

Examination of Figure 1 reveals a gradual rise in MBT of *Uta* from spring to autumn. Although not significant (Table 3), the rise in MBT seems to support a hypothesis of seasonal acclimatization to rising temperatures. Data available on seasonal metabolism (Roberts, 1968), however, fails to show acclimatization in spring, summer, or autumn lizards.

In winter, the side-blotched lizard's MBT is significantly lower than any other season (Fig. 1, Table 3). My data are insufficient to indicate whether the observed lowering of MBT represents a shift in preferred temperature of *Uta*, or whether the winter MBT is simply the lower end of the normal range of the species. McGinnis (1966) and Mayhew (1963) reported similar changes in T_b in two species of *Sceloporus*. McGinnis (1966) demonstrated that winter-active *Sceloporus occidentalis* had the same mean preferred temperature (MPT) as summer-active lizards when tested in a laboratory thermal gradient. Regal (1967) described voluntary hypothermia in a number of reptiles tested in a laboratory gradient, but did not test *U. stansburiana*. Roberts (1968) examined T_b and O_2 consumption in *Uta* throughout the year. She observed that MBT of winter-active lizards was reduced, and that they seemed to prefer the lower range of available temperatures in the field. Her winter-collected lizards showed an increase in O_2 consumption which suggested either acclimatization to low temperature or residual effects from summer juvenals. Dawson and Bartholomew (1956), on the other hand, were unable to demonstrate temperature acclimation in *U. stansburiana* in the laboratory. I feel that the available data strongly suggest acclimatization of *Uta stansburiana* to gradual seasonal changes in environmental temperatures.

In addition to their differential responses to thermal factors, the lizards studied at Saratoga Springs also respond differentially to other environmental factors, although not in so clear-cut a manner. All of the species examined seem to respond negatively to rain. The differences noted are generally in intensity of response, rather than type. Cloud cover that reduces insolation, hence environmental temperature, appears to affect the smaller species (*Uta*) before the larger. Wind, on the other hand, produces a negative response in *Dipsosaurus* before *Uta*. This probably results from *Uta* being able to utilize small, wind-free portions of the environment that are not available to *Dipsosaurus* because of its larger size. *Cnemidophorus* at Saratoga Springs apparently shift to more sheltered areas in response to wind before ceasing activity. *Callisaurus* seem to withstand more wind than any other species before reducing activity.

This study indicates, then, that the lizard species studied are segregated within the environmental components examined. The pattern of differential responses is complex and apparently has produced maximal environmental utilization with minimal interspecific interaction. The thermal partitioning just discussed is the most obviously differentiated environmental component studied. Other data on spatial and temporal relationships of these species at Saratoga Springs (Kay, m. s.) indicate that the species most similar in thermal requirements are quite clearly segregated in one or both of the others.

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